VARIABILITY IN FLOWER-NUMBER IN VERNONIA MISSURICA RAF.

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IN studying the species of *Vernonia* in the western states, the writer was impressed as early as 1903 by the constancy with which the number of flowers in each head of certain species agrees with the numbers of the Fibonacci series. This appeared at the time to be particularly true of *Vernonia fasciculata,* which normally presents 18 to 21 flowers. Extending his studies later to the species of tropical America, he found a still closer agreement with the Fibonacci series in the species with fewer-flowered heads, where the numbers 8 and 13 are repeated with little or no variation in several species. Inspired by the more recent studies of Stout and Boas,[1] who reported a steady seasonal decrease in flower-number in the heads of *Cichorium Intybus,* he again examined in 1918 a series of specimens of *Vernonia missurica,* the only species native in the vicinity of Ann Arbor, Mich., and made careful determinations of the number of flowers in every head of several plants, chosen from different localities and habitats. The results of these studies are presented here.

In the western part of its range, from Kansas to Illinois, *Vernonia missurica* is essentially a prairie species and is seldom or never found in woods or swamps. In Indiana it is excessively common on rolling hills in clay soil, preferring land formerly wooded but now used for pasture, where it is apparently avoided by live-stock. In the extreme eastern end of its range, in southeastern

[1] Stout, A. B., and Boas, H. M., "Statistical Studies of Flower Number per Head in *Cichorium Intybus;* Kinds of Variability, Heredity and Effects of Selection," *Mem. Torrey Club,* 17, 334–458, *pl. 10–13 + f. 1,* 1918.

Michigan and adjacent Ontario, it is typically a species of moist, cleared, uncultivated bottom-lands along the rivers and lakes and occasionally is found in low woods as well, where it is taller and more slender, with relatively lax, irregular, few-headed inflorescences. Judged from herbarium evidence from all parts of its range, the mode of its flower-number seems to be 34. Since flower-numbers deviate more freely from the Fibonacci series in the higher numbers and since the species has such a wide range and such a wide variation in its habitat, it may naturally be expected that it will present a wider variation in flower-number than many other species of restricted range and habitat and with smaller heads.

The inflorescence of the species may be described in some detail. It is strictly cymose. The main axis of the plant is unbranched and rises to a height of one to two meters. The lower nodes bear full-sized foliage leaves and are separated by internodes of fairly uniform length, while the upper internodes are abbreviated and bear reduced or bracteal leaves only. The main axis terminates in a single head on a short peduncle, and this head is the first, or among the first, to bloom. From the axils of the uppermost leaves branches appear which are in turn terminated by a single head on a longer peduncle, which therefore overtops the primary head. The next nodes, subtended by larger leaves, bear short simple leafless cymes of 2–5 heads. Below these, leafy branches appear from the lower nodes, and these bear single primary terminal heads, axillary heads on longer peduncles, and simple cymes in the same order in which they appear at the summit of the main axis. The uppermost of these leafy branches, since they arise relatively near the summit of the plant, also overtop the main axis and with it produce a more or less flattened or depressed corymbiform cluster. The lower lateral leafy branches are successively shorter, bear fewer heads which bloom later, and tend to produce in conjunction with the upper ones a more or less cylindrical cluster. Finally, the lowest

nodes bear short and frequently undeveloped lateral branches, which usually appear so late in the season that none of their heads, or only a part of them, open their flowers before frost. In many plants only the uppermost nodes bear branches at all, and in such cases the inflorescence is flattened or depressed. Every plant normally bears the primary terminal head and few or several subterminal heads and simple cymes from the uppermost axils. The number of heads is at a minimum in shady situations. The middle nodes bear floriferous branches only on large plants of favorable situations, where there is sufficient light and the plants are not crowded for space.

A single cyme consists of two or more heads on peduncles 1–3 cm. long with subulate bracts. Each peduncle is usually accurately curved and leaves the straight axis at a prominent angle, so that the true terminal heads are easily recognized. The usual number of heads in each cyme is two to five and the maximum number observed is nine. A cyme of two heads consists of a terminal head and an inferior lateral head. A cyme of three heads consists of the terminal and (*a*) two inferior lateral heads or (*b*) an inferior two-headed cluster. A cyme of four heads presents the usual terminal head and (*a*) three inferior lateral ones on separate peduncles or (*b*) one lateral head and one two-headed cluster. One of five heads has the true terminal and (*a*) a single inferior lateral head and a three-headed cyme of either of the types mentioned above or (*b*) two two-headed clusters. Cymes of greater numbers of heads have the same general structure, of a single terminal head with various combinations of single inferior heads, two-headed clusters and three-headed clusters.

Three types of variation were looked for in examining the species: (1) a variation between the heads of each cyme, possibly correlated with their position, whether terminal or inferior; (2) a variation between different floriferous branches of the same plant, possibly correlated with the amount of available nourishment; and (3)

a general variation between different individuals, possibly correlated with the size and vigor of the plant and therefore indirectly with the habitat.

1. Within a single cyme of 2–6 heads, the terminal head is usually the largest. In larger cymes of 7–9 heads some of the secondary terminal heads, ending the lower lateral branches of the leafless cluster, are frequently larger than the primary terminal head.

Table I exhibits the number of flowers in the terminal

TABLE I

RELATION OF FLOWER-NUMBER TO POSITION ON THE BRANCH

Branch	Primary Terminal	All Other Heads		
		Number	Largest	Average
1	46	1	46	46
3	59	5	53	49.6
4	56	5	53	51.0
6	57	8	55	51.4
8	54	4	50	48.5
9	53	5	51	49.2
10	57	12	54	51.1
11	55	13	55	49.5
12	57	10	55	49.3
13	57	8	54	50.4
14	58	9	56	52.6
15	56	18	58	53.1
16	52	14	57	52.9
17	55	14	59	52.1
18	50	21	58	52.9
19	54	22	60	53.4
20	54	16	56	52.4
21	54	14	56	51.7
22	52	15	60	52.9
24	59	8	62	53.0
25	57	5	55	53.8
26	53	2	50	48.5
27	50	3	52	49.7
28	53	2	53	50.0
29	52	1	50	50.0

head and the average number in the other heads on each of 25 floriferous branches from the same plant, the numbers beginning at the base. On 4 branches, numbers 2, 5, 7 and 23, the terminal head was defective or worm-eaten, and these have been omitted in the table. On 22 branches of the 25, the primary terminal head is larger than the average of the other heads and the difference may be as

much as 9.4. On 15 branches the primary terminal is actually the largest head on the branch. In 3 cases the primary terminal is smaller than the average, and in 10 cases it is exceeded in size by one or more of the lateral heads. It will be noticed that these conditions occur only on branches with numerous heads, where the terminal heads of certain individual cymes tend to raise the average. In fact, on those branches which bear a total of less than ten heads, and in which there are accordingly fewer chances for large secondary terminal heads, the average sizes of the two classes are 55 and 50.8 and with two exceptions (branches nos. 24 and 27) the primary terminal is actually the largest head on the branch. On branches with a total of 10–20 heads the averages are 55 and 51.9 and the primary terminal is actually the largest in only two fifths of the branches. In the two cases with over 20 heads the averages are 52 and 53.2 and the primary terminals are conspicuously exceeded in size by some of the other heads. Since the heads of each cyme differ but little in age, the variation in their size may possibly be due to difference in the amount of food-stuff or water available, by which the terminal heads at the end of a continuous axis are favored.

2. It has already been stated that the solitary heads and the floriferous branches appear in basipetal order and that those from the lowest nodes may not be sufficiently developed to bloom before frost stops all further growth. Table II shows the variation in flower-number correlated with the position of the branch.

The table indicates a steady increase in the number of abortive heads from the older branches at the summit to the younger ones at the base. The greatest number of heads are found near the middle of the series on the longest lateral branches, which rise from the middle internodes to a height equal to or surpassing the summit of the stem. But the average number of flowers is remarkably constant throughout, varying only from 50.7 to 52.9 for each set and, in general, reaching the maxi-

mum among the larger branches. It is obvious that there is very little relation between position and flower-number and the same conclusion is supported by the data from other plants.

TABLE II

RELATION OF FLOWER-NUMBER TO POSITION OF BRANCH

Branch	Number of Heads				Number of Flowers			Average by Groups
	Defective	Abortive	Fertile	Total	High	Low	Average	
1	0	10	2	12	46	46	46.0	
2	0	11	0	11				Fertile heads 3.2
3	1	16	6	23	59	47	51.2	Abortive heads 10
4	1	10	6	17	56	47	51.8	Flower-number 50.7
5	0	3	0	3				
6	0	10	9	19	57	47	52.0	
7	1	8	6	15	53	47	49.5	Fertile heads 8.6
8	0	5	5	10	54	47	49.6	Abortive heads 7.8
9	3	7	6	16	53	48	49.8	Flower-number 50.8
10	0	9	13	22	57	48	51.5	
11	0	6	14	20	55	45	49.9	
12	0	9	11	20	57	45	50.0	Fertile heads 13.4
13	3	5	9	17	57	47	51.1	Abortive heads 6.2
14	1	4	10	15	58	48	53.1	Flower-number 51.6
15	0	7	19	26	58	47	53.3	
16	0	1	15	16	57	49	52.9	
17	0	4	15	19	59	47	52.3	Fertile heads 18.8
18	1	5	22	28	58	46	52.8	Abortive heads 3.8
19	0	7	23	30	60	47	53.4	Flower-number 52.8
20	1	2	17	20	57	47	52.5	
21	2	2	15	19	56	48	51.9	
22	3	1	16	20	60	49	52.8	Fertile heads 12.4
23	3	0	8	11	58	47	53.0	Abortive heads 1.2
24	0	1	9	10	62	48	53.7	Flower-number 52.9
25	0	2	6	8	57	52	54.3	
26	1	0	3	4	53	47	50.0	
27	0	0	4	4	52	46	49.8	
28	0	0	3	3	53	47	51.0	
29	0	0	2	2	52	50	51.0	Fertile heads 2.1
30	0	0	1	1			55	Abortive heads 0
31	0	0	1	1			52	Flower-number 51.0
32	0	0	1	1			49	
33	0	0	1	1			56	
Total ...	21	145	278	444	62	45	52.1	

3. The number of maturing heads and the minimum, maximum, and average number of flowers per head in 22 plants is exhibited in Table III. Of these plants, numbers 1–18 inclusive were collected from a variety of

habitats and stations, in shade and sun, and in relatively wet and relatively dry soils. They show in every case a small variation within each plant, but a great variation between different plants, the averages ranging from 29.3 to 52.1. It happens that the plant with the largest number of heads also presents the highest flower-number, but in general there is no correlation between them, and

TABLE III

VARIATION IN FLOWER-NUMBER ON DIFFERENT PLANTS

Plant	Number Heads	Number of Flowers		
		High	Low	Average
1	278	62	45	52.1
2	26	43	37	40.0
3	26	41	34	37.3
4	15	38	29	31.9
5	14	36	27	31.9
6	31	40	31	36.4
7	19	45	37	42.2
8	25	39	32	35.4
9	95	37	22	29.3
10	62	35	26	29.7
11	43	39	28	34.2
12	15	51	45	47.7
13	7	36	32	34.0
14	11	45	36	40.5
15	3	46	44	45.0
16	19	38	34	35.5
17	3	39	35	37.0
18	33	34	26	29.4
19	126	38	26	32.5
20	98	37	26	32.2
21	61	38	27	32.0
22	74	36	25	32.7

the third highest average is presented by the plant with the smallest number of heads.

The last four plants, numbers 19–22, were collected from the same station and grew under similar environmental conditions in the usual (and for the region probably also the optimum) habitat of the species. They also present very similar averages in their flower-number. Others of the same station were also examined and demonstrated that essentially the same averages were repeated throughout the group.

From an examination of this table and from additional

experience with the plants, the writer is led to the tentative idea that two sets of factors, which may be environmental, or hereditary, or both, act on the plants independently, one determining the number of heads produced and the other the average number of flowers in each, so that there may result plants with many large heads (as no. 1), many small heads (no. 10), few large heads (no. 15), or few small heads (nos. 5, 18).

Table 4 shows the distribution of flower-numbers for all the heads of five plants. In each case the curves show a close relation to the main or secondary numbers of the Fibonacci series, 55, 29, 29, 34 and 34 respectively, although in only two cases do the modes fall precisely on these figures. Plant 1 shows a rather close grouping of heads just short of 55, plant 9 has over half of the heads grouped at 28–30, and plant 11 has almost half grouped at 33–35. It is scarcely to be expected that the series will be followed closely with such large numbers of flowers; in fact, Stout has demonstrated that there is no relation whatever to the Fibonacci series in the heads of *Cichorium Intybus*. Since the numbers were determined in every case by counting the mature achenes, the numbers should fall somewhat below the Fibonacci series, rather than above them, because of the possibility of some flowers not setting seed.

The plants used for these five tabulations were selected merely because of their large number of heads, which offer better data for developing a representative curve. Plants 20–22, with large numbers of heads also, agree closely with plant 19. A moment's inspection of the averages for the other plants, as shown in Table III, shows that in many cases, such as plants 2 and 3, they could not agree closely with the Fibonacci series, or that an apparent agreement might be fictitious if based on plants with a few heads only, as numbers 12 and 13.

TABLE IV

DISTRIBUTION OF FLOWER-NUMBERS

Plant 1

No. of heads..	3	7	15	16	26	23	30	31	38	24	24	13	15	7	3	2	0	1
No. of flowers.	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62

Plant 9

No. of heads..	1	0	1	3	5	10	15	16	18	11	6	4	2	1	1	1
No. of flowers.	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37

Plant 10

No. of heads..	2	1	15	16	9	9	6	1	2	1
No. of flowers.	26	27	28	29	30	31	32	33	34	35

Plant 11

No. of heads..	1	0	1	1	8	7	4	10	3	4	2	2
No. of flowers.	28	29	30	31	32	33	34	35	36	37	38	39

Plant 19

No. of heads..	3	5	4	11	8	12	6	16	37	11	9	3	1
No. of flowers.	26	27	28	29	30	31	32	33	34	35	36	37	38

SUMMARY

1. The number of flowers in each head is greatest for the terminal heads of each cyme.

2. Otherwise the number of flowers in each head is relatively constant for each individual plant.

3. There is a great variation between individuals but, in those plants with numerous heads, the mode falls on or near one of the main or secondary numbers of the Fibonacci series.